

# REDEFINITION OF THE *LITORIA LATOPALMATA* SPECIES GROUP (ANURA: HYLIDAE)

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## Summary

DAVIES, M., MARTIN, A. A. & WATSON, G. F. (1983) Redefinition of the *Litoria latopalmata* species group (Anura: Hylidae). *Trans. R. Soc. S. Aust.* **107**(2), 87-108, 31 May, 1983.

The *Litoria latopalmata* species group is composed of four terrestrial species characterized by unwebbed fingers, moderately webbed toes, poorly expanded finger and toe discs and variously developed lateral head stripes. The calls of all species are complex and consist of both short and long notes that are quite distinctive. Larvae of each species are very similar and of typical *Litoria* lentic form with  $\frac{2}{3}$  tooth rows. Osteology is conservative and differences between species are slight. Morphological characters separating species include rugosity of the skin, size of finger and toe discs, development of head and tibial stripes and differential thigh markings. Species included in the group are *Litoria latopalmata* Günther, *L. inermis* (Peters), *L. tornieri* (Nieden) and *L. pallida* sp. nov. The species group has been redefined in the light of morphological, call, larval and osteological data presented.

KEY WORDS: Anura, Hylidae, *Litoria*, morphology, osteology, larvae, mating calls, distribution.

## Introduction

The Australopapuan hylid frog genus *Litoria* Tschudi is a heterogeneous assemblage of species including frogs that can be described as 'tree frogs', with greatly expanded finger and toe discs and extensive webbing, as well as terrestrial species with unexpanded discs, long limbs and poor webbing. These latter species were called 'ground hylids' by Moore (1961).

Amongst the ground hylids is a homogeneous collection of species referred to as the *Litoria latopalmata* species group by Tyler and Davies (1978). The group includes *L. latopalmata* Günther, *L. inermis* (Peters) and *L. tornieri* (Nieden). The former two species have been recorded as having an extremely wide geographic range across north and east Australia (Moore 1961, Tyler 1968b, Straughan 1969, Cogger 1979, Barker and Grigg 1977). Tyler (1977) reported the occurrence of *L. latopalmata* in South Australia. Many of these authors have suggested that specimens referred to *L. latopalmata* may represent more than one species.

Here we redefine the described species and describe one new species referable to the *L. latopalmata* species group, based on our studies of comparative morphology, osteology and breeding biology.

## Materials and Methods

The specimens reported here are deposited in institutions abbreviated in the text as follows: AM, Australian Museum, Sydney; AMNH, American Museum of Natural History, New York; BMNH, British Museum (Natural History), London; KU, University of Kansas, Museum of Natural History, Kansas; NTM, Northern Territory Museum, Darwin, QM, Queensland Museum, Brisbane; SAM, South Australian Museum, Adelaide; WAM, Western Australian Museum, Perth; QPN, Queensland National Parks and Wildlife Service; RMNH, Rijksmuseum van Natuurlijke Historie, Leiden; UAZ, University of Adelaide, Department of Zoology. UAZ specimens are all cleared and stained skeletal preparations.

Methods of measurement follow Tyler (1968a) and osteological descriptions follow Trueb (1979). Tadpoles were fixed in Tyler's (1962) fixative and staged according to Gosner (1960). Osteological specimens were cleared and stained for bone after Davis & Gore (1947). Measurements were made using dial calipers or an eyepiece micrometer.

Measurements taken of adults were: snout to vent length (S-V); tibia length (TL); head length (HL); head width (HW); eye to naris distance (E-N); internarial span (IN); eye diameter (E); tympanum diameter (T). The following ratios were calculated: TL/S-V; HL/HW; HL/S-V; E-N/IN. Total length (tl) and body lengths (bl) of larvae also were re-

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corded. Where appropriate, means  $\pm$  S.D. are given.

Calls were recorded using a Sony TC 510-2, Uher 4000 or Sharp 4D492 tape recorder with dynamic microphones. Wet-bulb air temperatures were measured with a Schultheis quick-reading thermometer close to the calling sites of males. Calls were analysed by means of a sound spectrograph (Kay Model 6061-B Sonagraph) with the overall response curve maintained in the FL-1 position. Temporal characteristics of calls were determined from wide-band (300 Hz bandpass) and spectral characteristics from narrow-band (45 Hz bandpass) spectrograms. Two or three examples of each kind of call note given by each male were analysed and mean values were calculated.

Calls of all of the species examined share the same general structure. Two distinct kinds of note are produced; these we have designated 'long calls' and 'short calls'. Each male typically emits call notes in long sequences, usually commencing with short calls and then switching to the production of long calls. Occasionally there are also notes which appear transitional between short and long calls, but we have not attempted to analyse such transitional notes. For each species we present

analyses of what we consider to be typical short and long call notes. Most calls are well-tuned, with harmonic bands across a fairly wide frequency range. We have taken the dominant frequency as the band or bands containing the most energy. Although our call samples are clearly inadequate, the data are included because they assist specific diagnoses.

The following abbreviations are used in locality data: S.F., State Forest, N.P., National Park, Ck, Creek, Hstd, Homestead.

*Litoria latopalmata* Günther

FIGS 1-7

*Litoria latopalmata* Günther 1867, *Ann. Mag nat. Hist. ser. 3*, 20:55

*Hyla latopalmata*: Boulenger 1882, p. 414; Nieden 1923, p. 227

*Hyla palmata*: Slevin 1955 (lapsus pro *Hyla latopalmata*) p. 383

*Litoria latopalmata*: Tyler 1971 (*partim*), p. 353

*Definition*: A moderately small, ground-dwelling species (females 36-42 mm, males 29-39 mm) characterised by unwebbed fingers with slightly expanded discs, first finger slightly longer than second, moderately long hind



Fig. 1. *Litoria latopalmata*, in life (Watagan, S. F., N.S.W.).

limbs (TL/S-V 0.57–0.75), well developed lateral headstripe with white preocular bar, grey or brown dorsum, occasionally mottled. *Redescription*: based on SAM R19717, a mature male collected north of Maryborough, Qld by K. R. McDonald on 10.xii.1977.

Head broader than long (HL/HW 1.23). Head length more than 1/3 snout to vent length (HL/S-V 0.40). Snout prominent,

projecting in profile (Fig. 1), sharp when viewed from above and very gently rounded in profile. Nostrils more lateral than superior, their distance from end of snout about 2/3 that from eye. Distance between eye and naris less than internarial span (E-N/IN 0.97). Canthus rostralis well defined and straight, its nature accentuated by dark rostral stripe. Eye moderately conspicuous, its dia-

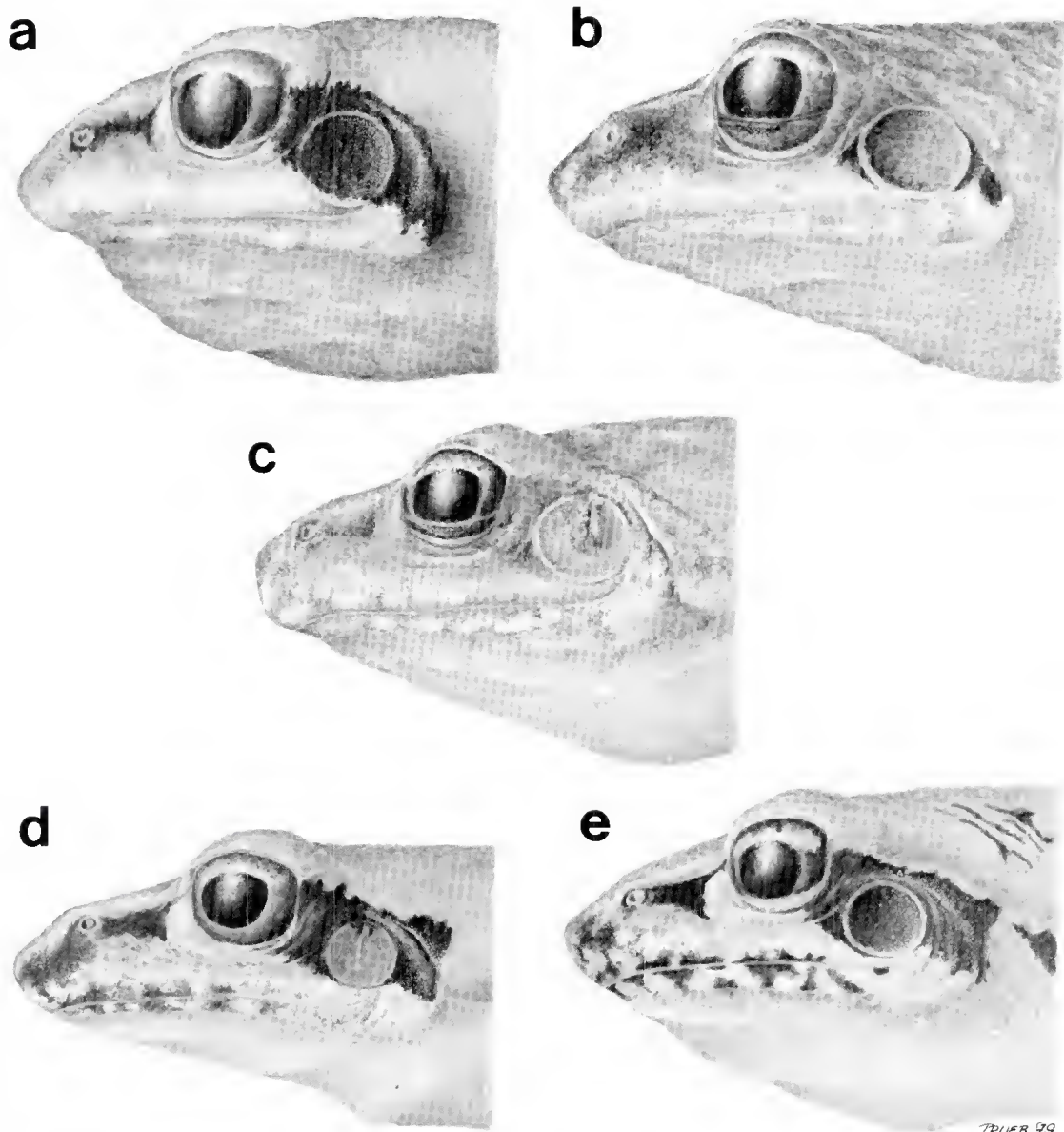


Fig. 2. Lateral view of the heads of a, *Litoria pallida* (SAM R19539), b, *L. inermis* (from Qld, SAM R19558), c, *L. inermis* (from W. Aust.), d, *L. tornieri* (SAM R19572) and e, *L. latopalmata* (SAM R19682).

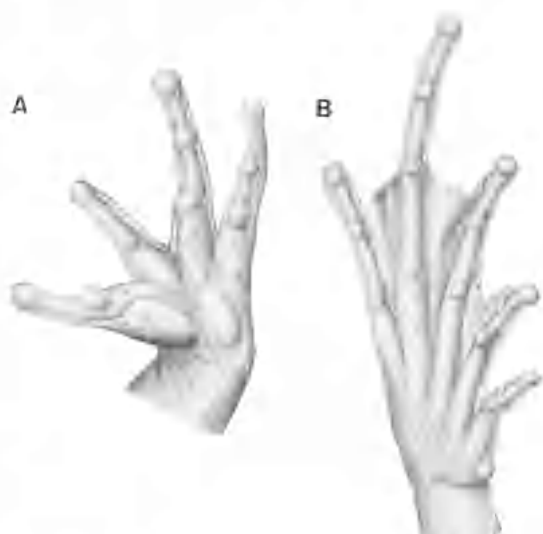


Fig. 3. A, Palmar view of hand and B, plantar view of foot of *Litoria latopalmata* (SAM R19539).

meter about 1/3 longer than eye to naris distance. Tympanum completely visible, its diameter  $\frac{2}{3}$  eye diameter (Fig. 2).

Vomerine teeth on short oval projections at 45° to choanae. Tongue broadly oval. Fingers long and slender, slightly fringed (Fig. 3A); in order of length  $3 > 4 > 1 > 2$ . No webbing between fingers. Terminal discs slightly expanded just extending laterally beyond the fringes of the penultimate phalanx. Subarticular and palmar tubercles prominent. Small supernumerary tubercles present.

Hind limbs long (TL/S-V 0.65). Toes in order of length  $4 > 3 > 5 > 2 > 1$  (Fig. 3B). Webbing reaches midpoint of penultimate phalanx on toe 5 and to subarticular tubercles at base of antepenultimate phalanx on toe 4. Subarticular tubercles prominent. Well developed supernumerary tubercles on metatarsals 3 and 4. Small oval inner and tiny, round, outer metatarsal tubercles.

Dorsum smooth, abdomen, pectoral region ventral and posterior thighs coarsely granular. Submandibular area smooth. Well developed tarsal and supratympanic folds.

Dorsum grey; conspicuous lateral headstripe from nostril to eye, interrupted by cream preocular bar, extending behind the eye over and through the tympanum to the insertion of the forearm. Thin white line extends from below eye to end of mandibular region. Disrupted dark patches extend to flanks. Mandibular margin variegated with dark and light

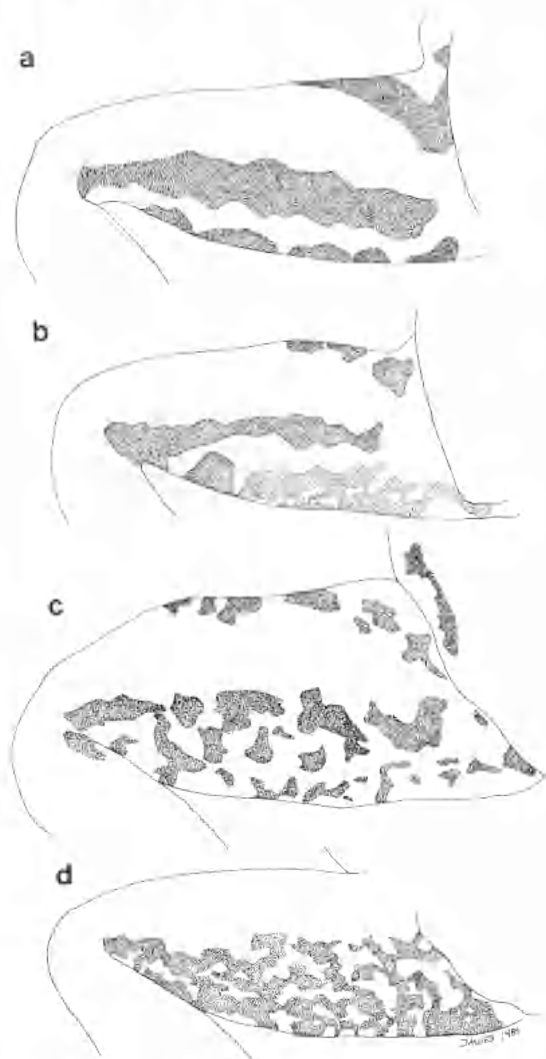


Fig. 4. Backs of thighs showing pigment reticulations: a, *Litoria pallida*, b, *L. tornieri*, c, *L. latopalmata*, d, *L. inermis*.

patches which extend around upper jaw. Faint dark patch present on wrist.

Backs of thighs pale yellow with discrete patches of brown pigmentation (Fig. 4). Thin disrupted dark stripe along anterior edge of tibia and tarsus, and on plantar surface of tarsus and foot.

Gular region lightly suffused with pigment. Brown bilobed nuptial pad present.

*Material examined:* BMNH 1947.2.24 (syntype) Port Denison (Bowen) Qld. Queensland: SAM R19711-29 N of Maryborough; SAM R19694-19710, Conondale Ra., QPN N28404, N28434, N28454-63, N28472 Ambathala Nature Reserve; SAM R19671-81, Bellthorpe, S. F., Conondale Ra., SAM R19683-93, Eungella N.P.; QM J31364,

J31370, Conondale Ra.; QM J31374-5, below Boombana N.P., Mt. Nebo Rd.; QM J35796, Ferguson, 6 km N of Maryborough; UAZ A66, Eungella N.P.; UAZ A67-8, A522, Bellthorpe S. F., Conondale Ra.; UAZ A521, Ambathala Nature Reserve; N.S.W.; SAM R12200-2, Ulong; SAM R19670, Penshurst; SAM R19669, Sherwood S. F.; SAM R12196-9, Camden; SAM R12194-5, Tumby Umbi; QM J31376-8, Back Creek Rd off Tenterfield-Bonshaw Rd.; S.A.; SAM R15840, Moomba.

#### Variation

Head broader than long (HL/HW  $1.24 \pm 0.05$ , 1.10-1.40); head length greater than 1/3 snout to vent length (HL/S-V  $0.39 \pm 0.02$ , 0.34-0.42). Distance between eye and naris usually less than internarial span ( $0.94 \pm 0.10$ , 0.77-1.38).

Hind limbs consistently long (TL/S-V  $0.64 \pm 0.03$ , 0.56-0.75). Dorsum grey or mottled. Tibial stripe interrupted in many specimens, but entire in others.

#### Osteology

Skull moderately well ossified with well ossified neurocranium. Sphenethmoid well ossified extending between nasals dorsally almost to their anterior extremities, ventrally extending anteriorly to dentigerous processes of prevomers. Nasals overlying sphenethmoid along their medial edges (Fig. 5A). Prootic and exoccipital fused. Exoccipital entire. Crista parotica well developed, moderately long and stocky. Otic ramus of squamosal

expanded posteriorly, just articulating with distal edges of crista parotica.

Frontoparietal fontanelle extensive, extending anteriorly to level of palatines, posteriorly to suture of frontoparietal and exoccipital region. Orbital edges of frontoparietals straight. Nasals moderately large, maxillary processes acuminate, not articulating with well developed preorbital processes of pars facialis of maxillary.

Palatines moderately long, expanded distally, tapering more medially to overlie sphenethmoid. Parasphenoid robust, cultriform process subacuminate, long, almost reaching to level of palatines. Alae broad, at right angles to cultriform process, expanded distally, and overlapped by medial arm of pterygoid (Fig. 5B).

Pterygoids moderately robust, anterior arm in short contact with palatal shelf of maxillary. No obvious pterygoid process of palatal shelf. Medial arm well developed, rounded terminally. Quadratojugal slender and fully articulated. Squamosal moderately robust; zygomatic ramus acuminate, slightly shorter than otic ramus. Maxillary and premaxillary dentate.

Pars facialis moderately shallow, well developed preorbital process. Alary processes of premaxillaries elongate laterally and curved posterolaterally. Palatine processes of premaxillaries well developed, not abutting medially. Prevomers slightly reduced medially, with short dentigerous process slightly angled to midline. Bony columella present.

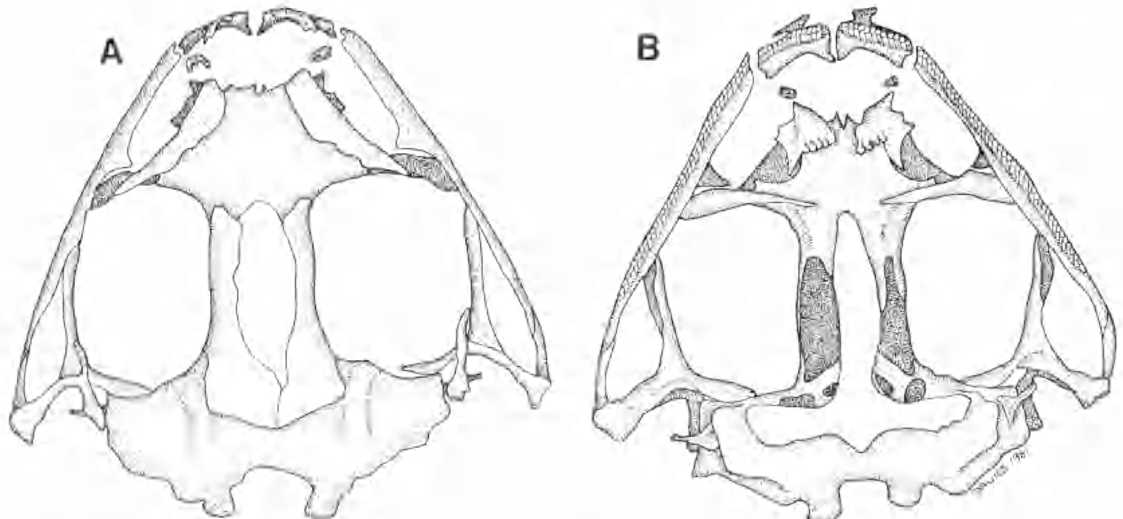


Fig. 5. A, Dorsal and B, ventral views of skull of *Litoria latopalmata* (UAZ A522).

TABLE 1: Physical characteristics of calls of males of the *L. latopalmeta* species group. Mean values are given with ranges in parentheses. PRR = pulse repetition rate. Details of localities are: 1, 30 km W Coonabarabran, NSW, 20.x.1964; 2, Mitchell Plateau, W. Aust., 27.i.1978; 3, Coen Airport, Qld, 7.iii.1979; 4, Lakefield N.P., Qld, 25.ii.1981; 5, Gulungul Ck Crossing, Arnhem Highway, N.T., 1.ii.1979; 6, Birndu, N.T., 30.xi.1978.

Species, locality and date	N	Short Call				Long Call				Wet bulb temp.
		Duration msec	No. of pulses	PRR pulses/sec	Dom. freq. Hz	Duration msec	No. of pulses	PRR pulses/sec	Dom. freq. Hz	
<i>L. latopalmeta</i> 1	1	52.5 (45-60)	7 (6-8)	114 (111-117)	2900	88.3 (85-90)	12 (11-13)	124.3 (118-133)	2900	9.5
<i>L. inermis</i> 2	1	37	7.5 (7-8)	175.5 (162-189)	3000	175 (165-185)	39.7 (37-41)	221 (216-229)	3300	24.0
3	1	27.3 (27-28)	7	219.3 (214-222)	4250	66.7 (60-75)	17.7 (16-20)	249.7 (246-253)	3850	24.8
4	1	36 (35-37)	8	194.3 (189-200)	4300	105 (100-110)	27.7 (27-29)	254.3 (248-260)	4100	25.4
<i>L. tornieri</i> 5	2	68.3 (65-70)	11.3 (10-12)	150.8 (138-157)	2000	128.3 (115-140)	23.8 (22-25)	178.2 (171-183)	1850	25.0- 26.0
6	1	59 (57-60)	10	152.7 (150-158)	1950	198.3 (195-200)	35	176 (171-179)	1950	27.2
<i>L. pallida</i> 5	1	30	5.5 (5-6)	150 (133-167)	1500	337.5 (330-345)	63.5 (61-66)	185 (182-188)	1500, 3300, 4000	25.0
3	1	22.5 (20-25)	3.5 (3-4)	110 (100-120)	1450, 4150	455 (450-460)	81.3 (78-84)	176.3 (171-180)	3400 4150	25.8

Pectoral girdle arciferal and robust. Omoternum and xiphisternum present. Clavicles moderately slender, slightly shorter than scapula and closely applied medially. Coracoids moderately separated. Suprascapula about 2/3 ossified.

Eight procoelous, nonimbricate, presacral vertebrae. Medial dorsal ossification incomplete on vertebrae I, II, III and IV. Relative widths of transverse processes: III > IV > V II > sacrum = VI > VII > VIII. Sacral diapophyses poorly to moderately expanded; ilia extend anteriorly beyond expansion. Bicondylar sacrococcygeal articulation. Well developed crest extending  $\frac{1}{2}$  length of urostyle.

Phalangeal formula of hand 3,3,4,4; well developed bony prepollux. Phalangeal formula of foot 3,3,4,5,4; well developed bony prehallux. Terminal phalanges claw shaped.

#### Variation

Prevomarine teeth are sometimes horizontally oriented, rather than slightly angled to midline. The maxillary processes of the nasals

occasionally articulate with the perorbital processes of the pars facialis of the maxillaries.

#### Breeding Biology

*Call*: Physical characteristics of the calls of a New South Wales male are shown in Table 1 and audiospectrograms of short and long calls in Fig. 6. This species shows the least differentiation between short and long calls; both are well-tuned notes. Caution must be used in comparing these calls with those of the other species because of the much lower recording temperature.

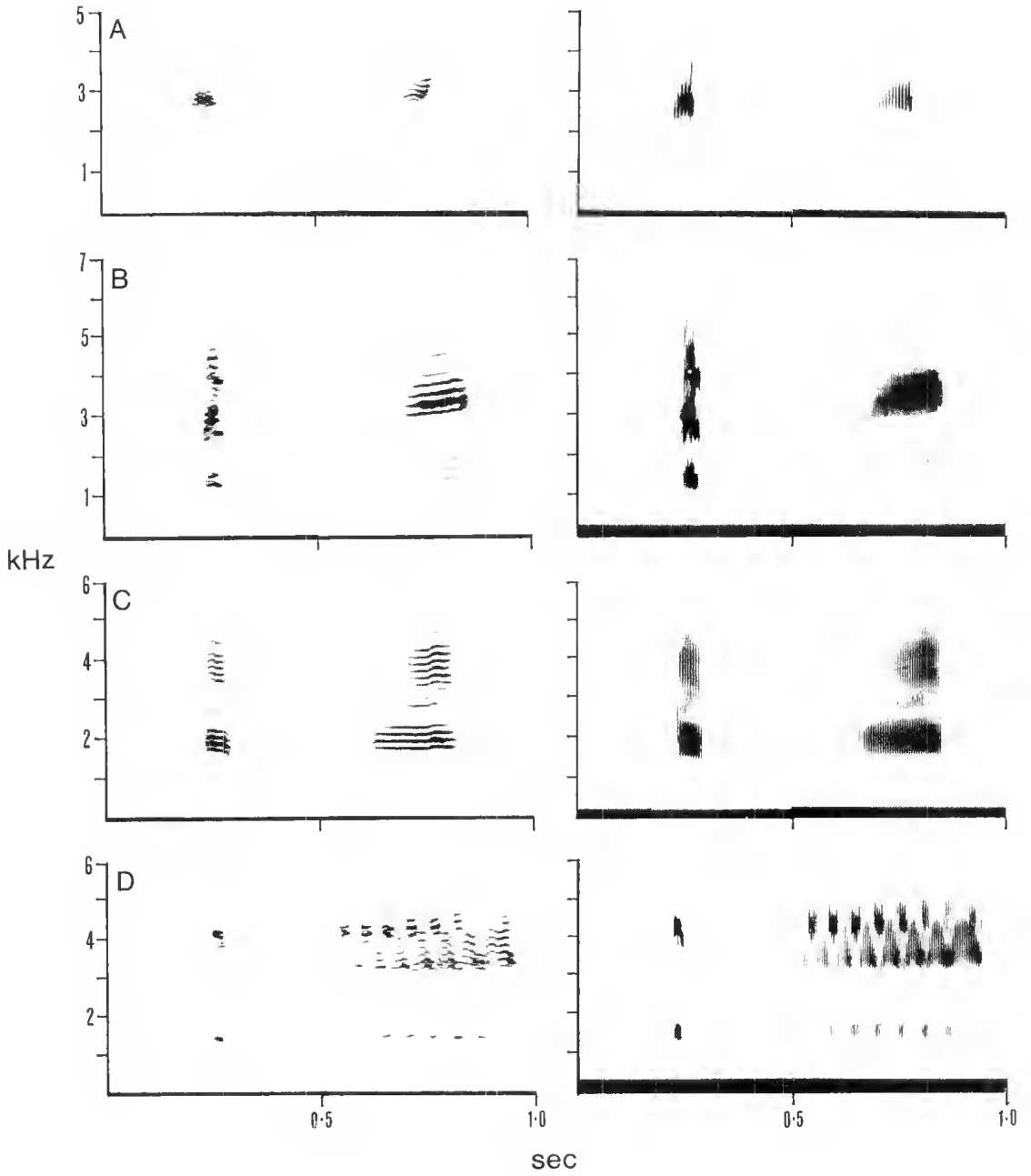
*Early development*: Unknown.

#### Distribution

This species is confined to eastern Australia (Fig. 7). The type locality is Port Denison (Bowen) Qld and the species extends south through Queensland to northern N.S.W. A specimen was collected at Gidgealpa Waterhole in South Australia in 1976 (Tyler, 1977).

*Litoria latopalmeta* is an open forest species breeding in temporary, summer rain-filled

Fig. 6. Audiospectrograms of calls of males of the *Litoria latopalmeta* species group. In each case the traces are, left to right: short call, 45 Hz bandpass; long call, 45 Hz bandpass; short call, 300 Hz bandpass; long call, 300 Hz bandpass. A, *L. latopalmeta*, 3 km W of Coonabarabran, N.S.W., wet bulb 9.5°C; B, *L. inermis*, Mitchell Plateau, W.A., wet bulb 24.0°C; C, *L. tornieri*, Birndu, N.T., wet bulb 27.2°C; D, *L. pallida*, Coen Airport, N.Q., wet bulb 25.8°C.



\* Spots and diagonal lines on 300 Hz bandpass of *C. L. tornieri* are trace damage artifacts.



Fig. 7. Distribution of *Litoria latopalmata* and *L. tornieri* in Australia. Open symbols indicate literature records and closed symbols specimens examined in this study. Stars indicate type localities. *L. latopalmata* records = circles, *L. tornieri* records = triangles.

pools. It is sympatric with *L. inermis* at many localities.

#### Comparison with other species

*Litoria latopalmata* can be distinguished from all terrestrial congeners, other than members of the *Litoria aurea*, *L. freycineti* and *L. latopalmata* species groups, by its poorly expanded finger discs. The members of the *L. aurea* group differ in gross habitus and size and the *L. freycineti* group have relatively longer hind limbs. *L. latopalmata* can be delineated from other members of its species group in the following ways. From *L. inermis*, *L. latopalmata* can be distinguished by its relatively smooth dorsum and well defined canthal stripe and from *L. tornieri*, by its longer hind limbs ( $TL/S-V$   $0.64 \pm 0.03$  compared with  $0.57 \pm 0.04$ ), slightly greater webbing between toes four and five and by the slight expansion of its finger and toe discs beyond the edges of the penultimate phalanges. *L. latopalmata* is distinguished from *L. pallida* by its larger size (28–37 mm male, 36–42 mm female, compared with 27–34 mm male, 31–37 mm female) and slightly expanded discs. *Litoria latopalmata* shows the least differentiation between long and short calls, with long calls being shorter than in all other species.

#### *Litoria inermis* (Peters)

FIGS 2, 4, 6, 8–13

*Chiroleptes inermis* Peters, 1867, *Mber. dt. Akad. Wiss. Berlin* 1867: 30

*Phractops inermis*: Nieden 1923, p. 524

*Cyclorana inermis*: Parker 1940, p. 17

*Hyla latopalmata*: Tyler 1968b (*partim*) p. 719

*Hyla inermis*: Straughan 1969, p. 208

*Litoria inermis*: Tyler 1971, p. 353

**Definition:** A small, ground-dwelling species (females 30–37 mm; males 24–33 mm) characterised by unwebbed fingers; poorly expanded terminal discs, first finger slightly longer than second, moderately long hind limbs ( $TL/S-V$   $0.59 \pm 0.04$ ,  $0.52-0.68$ ); indistinct headstripe; mottled tubercular dorsum. **Redescription** of syntype RMNH 1888. Rockhampton, Qld.

Head longer than broad ( $HL/HW$  1.18). Head length more than  $1/3$  snout to vent length ( $HL/S-V$  0.37). Snout prominent, projecting in profile (Fig. 8), slightly rounded when viewed from above and in profile. Nostrils slightly more lateral than superior, their distance from end of snout less than twice that to eye. Distance between eye and naris less than internarial span ( $E-N/IN$  0.83). Canthus rostralis very slightly defined and straight. Eye relatively small and incon-

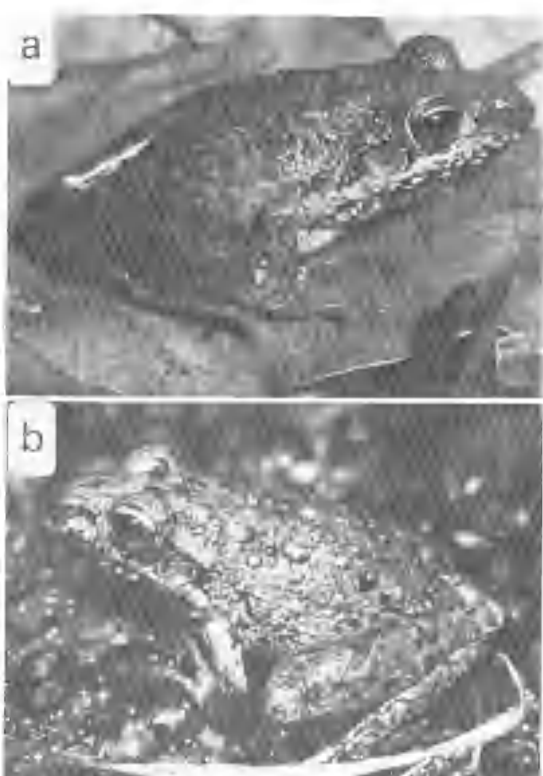


Fig. 8. *Litoria inermis* in life: a, Fossilbrook Ck, Qld and b, Borooloola, N.T.



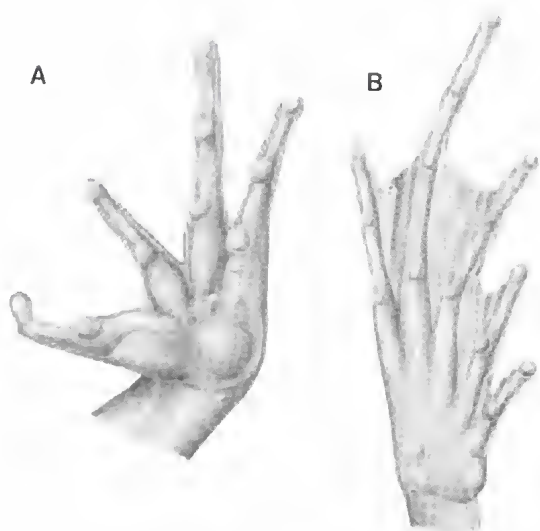


Fig. 9. A, Palmar view of hand and B, plantar view of foot of *Litoria inermis* (SAM R19558).

spicuous, its diameter greater than eye to naris distance. Tympanum completely visible, its diameter about  $2/3$  eye diameter (Fig. 2).

Vomerine teeth on short oval elevations at  $45^\circ$  to midline between choanae. Tongue broadly oval. Fingers long and slender, unwebbed with well developed fringes. In order of length  $3 > 1 > 4 > 2$  (Fig. 9A). Terminal discs poorly developed and not extending laterally beyond fringes. Subarticular and palmar tubercles prominent. Supernumerary tubercles on metacarpals not well developed.

Hind limbs long (TL/S-V 0.62). Toes in order of length  $4 > 3 > 5 > 2 > 1$  (Fig. 9B). Webbing not reaching midpoint of penultimate phalanx on toe 5 and to subarticular tubercle of antepenultimate phalanx on toe 4. Subarticular tubercles prominent. Small oval inner and rounded outer metatarsal tubercles. Dorsum weakly tubercular; abdomen and back of thighs finely granular; submandibular area smooth. Moderately developed tarsal fold and weakly developed supratympanic fold.

Colour in preservative: dorsum brownish with darker brown mottling. Very poorly developed indistinct lateral headstripe only visible behind eye through tympanum to level of forearm. Well developed cream mottled patch at angle of jaw; edge of mouth surrounded by white variegations with dark pigment granules. Hind portion of thighs reticulated brown on grey, ventral surface discoloured brown.

*Material examined:* Two syntypes: RMNH 1888, Rockhampton, Qld; AMNH 23582, Bowen, Qld and 184 additional specimens.

Queensland: SAM R19562-70, Fossilbrook Ck; SAM R19559-61, N of Maryborough; SAM R19557, Cape Hillsborough; SAM R19556, Mourangee Stn; SAM R12118-23, Leggitts Lagoon nr Cooktown; SAM R11033-4, Cooktown; QPN N32440-1, Coen; QPN N32341, 32347, Coen Airport; QPN N32494, Silver Plains Hstd; SAM R19571 (16) Eight Mile Ck floodplain, Conjuboy Stn; QM J27188-9, approx. 50 km S Winton; QM J27631, J32522, J32524, J32526, Alice R., 7 km S, 23 km W Townsville; QM J27688, J32536-8, J32540-2, Black R., "1 km D, 3 km E Yabulu; QM J35768, Ferguson Quarry 'via' Maryborough; QM J35770, Burgowan Minesite No. 13, E of Howard; QM J35771, Ferguson, 6 km N Maryborough; UAZ A237, Mourangee Stn, Eudungalba; UAZ A527 Mellwraith Ra.; UAZ A528, N of Maryborough; QM J41012, Lakefield N.P., at Lakefield Hst; QM J41011, Coen Airport.

Northern Territory: SAM R23285-300, SAM R23343-52, SAM R23312-25, R23352, R23284, Jabiru Airstrip; SAM R23303-10, Ja Ja Borrow Pit at Pan Continental Camp entrance; SAM R23327-9, McArthur R. on Bridge to McArthur River Stn; SAM R23302, Cannon Hill; SAM R23301, Surprise Ck, 40 km N McArthur R. Stn; SAM R9835, Berry Springs; SAM R9105 145 km N Mainoru; SAM R23283, 50 m N Retention Pond No. 2 Djalkmarra Ck; SAM R23338-42, Katherine R., 7 km W Katherine Gorge N.P., SAM R23326, 14 km N Katherine; SAM R23330-3, 13 km N Katherine; SAM R23311, 6.4 km N Katherine; SAM R23334-7, 4 km N Katherine; UAZ A616, 100 m E Jim Jim turnoff, Arnhem Highway; UAZ A617, Jabiru Airstrip; UAZ A618, Jabiru East turnoff, Arnhem Highway; NTM R10093-7, 4 km N Katherine.

Western Australia: UAZ A241-2, A529, Mitchell Plateau; UAZ A530, Parry Ck/Kununurra Rd; WAM R81873-83, Granite Ck, 16 km NE Lake Argyle Village; WAM R81884-88, Kununurra; WAM R81890-99, Mitchell Plateau; WAM R81889, Mitchell Plateau campsite; WAM R81901-2, Ivanhoe Crossing; WAM R81900, Hidden Valley, Kununurra; KU192460-4, Mitchell Plateau; KU192465, Four Mile Creek, 32 km ESE Kununurra.

#### Variation

Small frog (males 24-33 mm, females 30-37 mm S-V). Head longer than broad (HL/HW  $1.26 \pm 0.062$ ,  $1.11-1.40$ ). Head length  $1/3-1/2$  snout to vent length (HL/S-V  $0.39 \pm 0.017$ ,  $0.34-0.43$ ). Hind limbs long (TL/S-V  $0.59 \pm 0.044$ ,  $0.51-0.68$ ). E-N/IN highly variable ( $0.91 \pm 0.098$ ,  $0.73-1.21$ ).

The syntype is discoloured and soft. Freshly preserved specimens differ from it in the presence of supernumerary tubercles on all metacarpals, and in having coarsely to poorly tubercular grey dorsum mottled with black and brown patches. The lateral headstripe is always poorly developed, sometimes evident anteriorly to the eye and nostrils and through and above the tympanum posteriorly. The ventral surface is pale cream, back of thighs darkly pigmented with small patches of pale ground colour (Fig. 4).

### Osteology

Skull relatively fragile with moderately ossified neurocranium. Sphenethmoid moderately ossified extending between nasals for about  $\frac{1}{3}$  of their length dorsally; ventrally sphenethmoid not extending between prevomers. Nasals not overlying sphenethmoid. Prootic and exoccipital fused. Exoccipital not fused dorsomedially or ventromedially. Crista parotica moderately well developed, short and stocky, not articulating laterally with poorly expanded otic ramus of squamosal (Fig. 10A). Frontoparietal fontanelle extensive, rectangular extending anteriorly for about  $\frac{2}{3}$  orbit. Posterior margin of fontanelle not delineated because of lack of medial ossification of exoccipital. Orbital edges of frontoparietal straight.

Nasals moderately large. Maxillary process of nasals moderately sharp, not articulating with well developed preorbital process of pars

facialis of maxillary. Palatines moderately long, broad laterally, slender and acuminate medially, overlying sphenethmoid. Parasphenoid robust; broad cultriform process reaching almost to level of palatines; alae long, moderately broad, just overlapped by medial arm of pterygoid.

Pterygoid moderately well developed with anterior arm making short contact with palatal shelf of maxillary (Fig. 10B). No pterygoid process. Medial arm of pterygoid moderately long, not in bony contact with prootic region. Quadratojugal slender and fully articulated. Squamosal moderately robust. Otic ramus slightly longer than zygomatic ramus. Maxillary and premaxillary dentate. Preorbital process of moderately shallow pars facialis of maxillary well developed. Alary processes of premaxillaries elongate laterally and curved posteriorly. Palatine processes of premaxillaries well developed, not abutting medially. Prevomers reduced slightly anteromedially; not articulating or overlapping sphenethmoid. Dentigerous processes short, horizontally oriented. Bony columella present.

Pectoral girdle arciferal, moderately robust. Omosternum and xiphisternum present. Clavicles slender and abutting medially. Coracoids moderately separated. Scapula bicapitate, slightly shorter than clavicle. Suprascapula about  $\frac{2}{3}$  ossified.

Eight procoelous nonimbricate presacral vertebrae. Medial dorsal ossification incom-

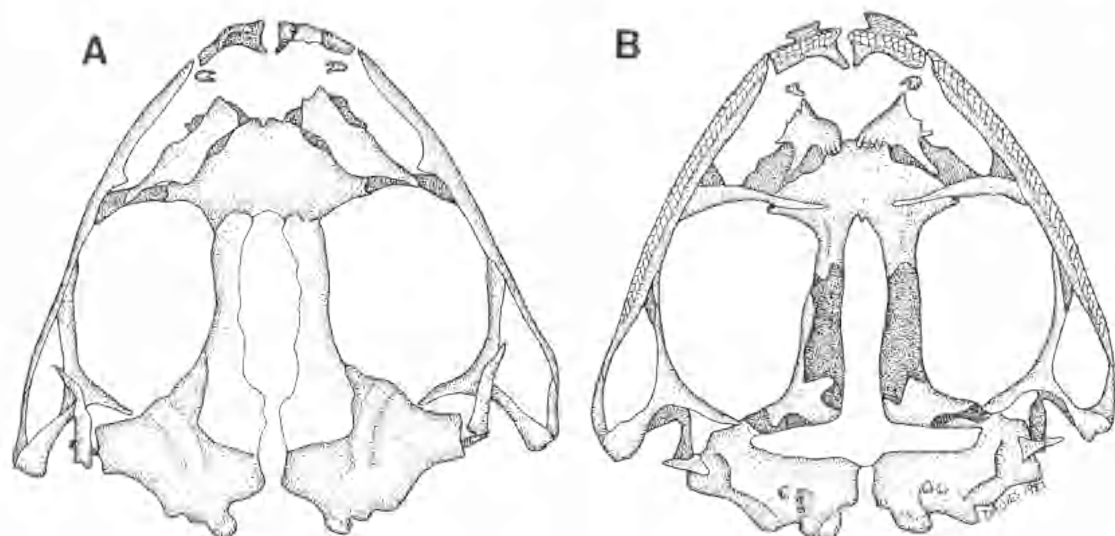


Fig. 10. A. Dorsal and B. ventral view of skull of *Litoria inornata* (UAZ A528).

plete on presacrals I, II and III. Relative widths of transverse processes: III > II > IV = sacrum > V > VI > VII > VIII. Sacral diapophyses moderately expanded, ilia extending anteriorly beyond expansion. Bicondylar sacrococcygeal articulation. Well developed crest extending  $\frac{1}{3}$  length of urostyle.

Phalangeal formula of hand 3,3,4,4; well developed bony prepollex. Phalangeal formula of foot 3,3,4,5,4; well developed bony prehallux. Terminal phalanges claw shaped.

#### Variation

Ossification of the sphenethmoid varies between specimens—the foregoing description applies to minimal ossification of the roofing

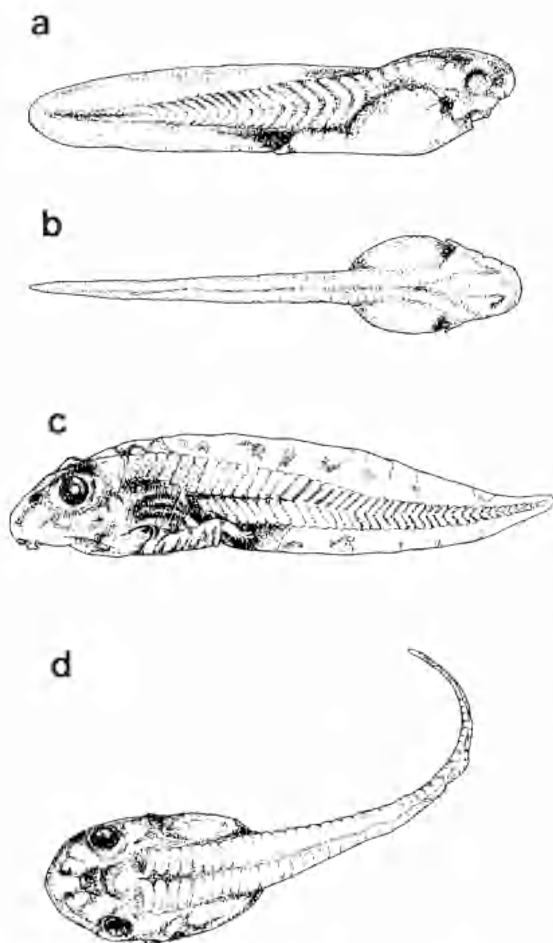


Fig. 11. a, Dorsal and b, lateral views of embryo at stage 20, and c, dorsal and d, lateral views of larva at stage 36 of *Litoria inermis*. Total length of embryo 4.5 mm, body length 1.9 mm, total length of larva 30.5 mm, body length 12.5 mm.



Fig. 12. Mouthparts of a larva, stage 37, of *Litoria inermis* from Blencoe Falls, Qld. Scale bar = 1 mm.

bones. In other specimens, the sphenethmoid is well ossified extending between and to the anterior extremities of the nasals dorsally and anteriorly to the vomerine teeth ventrally. Variation also occurs in the degree of crenulation of the medial edges of the frontoparietals and in the length of the cultriform process of the parasphenoid.

#### Breeding Biology

**Call:** *Litoria inermis* usually calls from open gravelly or sandy areas, often on steep sloping banks within 1–2 m of water. At Jabiru, males were heard calling between the middle of November and the middle of March (Tyler *et al.* 1983).

The short call is a staccato note with little tuning; the long call is at least twice the duration of the short call (Table 1, Fig. 6).

**Early development:** Described by Tyler *et al.* (1983). The morphology of embryos at stage 20 and larvae at stage 36 is shown in Fig. 11. The eyes are more dorsally situated than in larvae of other members of the complex. The mouthparts of a larvae at stage 37 are shown in Fig. 12.

#### Distribution

*Litoria inermis* is found across the north of Australia from Mitchell Plateau in W.A. to Cape York in Qld and south to Rockhampton (Fig. 13). Syntypes were collected at Rockhampton and Bowen in Queensland.

The species is an open forest dweller and tends to avoid thick grass, preferring open areas of sparse, low vegetation. In Queensland *L. inermis* is sympatric with *L. latopalmata*



Fig. 13. Distribution of *Litoria inermis* in Australia. Open symbols are literature records and closed symbols are specimens examined during this study. Stars indicate type localities.

and at Jabiru in the Northern Territory with both *L. tornieri* and *L. pallida*.

#### Comparison with other species

*Litoria inermis* can be distinguished from all terrestrial congeners, except for members of the *L. aurea*, *L. freycineti* and *L. latopalmata* species groups, by the poorly expanded terminal discs on its fingers and toes. It is distinguished from members of the *L. aurea* species group by gross size and habitus and from the *L. freycineti* group by its relatively shorter hind limbs. From *L. tornieri*, *L. latopalmata* and *L. pallida*, *L. inermis* is distinguished by its tubercular dorsum, finely reticulated thigh markings and poorly developed canthal streak. The pulse repetition rates of both long and short calls of *L. inermis* are higher than those of the other species in this group.

*Litoria tornieri* (Neiden)

FIGS 2, 4, 6, 7, 14–17

*Pelodytes affinis* Gray, 1842, *Zool. Misc.* London 3:56

*Hyla affinis*: Boulenger 1882 p. 413

*Hyla tornieri*: Nieden 1923 (nomen substitutum pro *Pelodytes affinis*) p. 228

*Hyla latopalmata latopalmata*: Copland 1957 (partim) p. 94

*Litoria latopalmata*: Tyler 1971 (partim) p. 353

*Litoria tornieri*: Cogger & Linder 1974 p. 71

*Litoria affinis*: Duellman 1977 p. 114

**Definition:** A small ground dwelling species (males 28–36 mm, females 27–34 mm) characterised by basal webbing between the fingers, poorly developed terminal discs, first

finger longer than second, moderately short hind limbs (TL/S–V  $0.57 \pm 0.04$ , 0.49–0.68), well developed lateral headstripe, continuous stripe along outside edge of tibia, smooth brown/grey dorsum, reddish in breeding season.

**Description:** Based on SAM R18686 a male specimen collected in a pool 800 m W of Gulungul Creek Crossing, Arnhem Highway, N.T. by G. A. Crook on 1.ii.1979.

Head longer than broad (HL/HW 1.30); head length more than 1/3 snout to vent length (HL/S–V 0.4). Snout prominent, projecting in profile; slightly rounded when viewed from above and in profile. Nostrils more lateral than superior, their distance from end of snout 2/3 that from eye. Distance between eye and naris less than internarial span (E–N/IN 0.84). Canthus rostralis slightly defined and curved, its nature accentuated by dark rostral stripe. Eye relatively small and inconspicuous, diameter about 1½ times eye to naris distance. Tympanum completely visible, diameter 2/3 eye diameter (Fig. 15).

Vomerine teeth on short elevations between choanae. Tongue broadly oval.

Fingers long and slender lacking lateral fringes; in order of length  $3 > 4 > 1 > 2$  (Fig. 14). Basal webbing between fingers 2 and 3 and 3 and 4. Terminal discs poorly developed, not extending laterally beyond the edges of penultimate phalanx. Subarticular and palmar

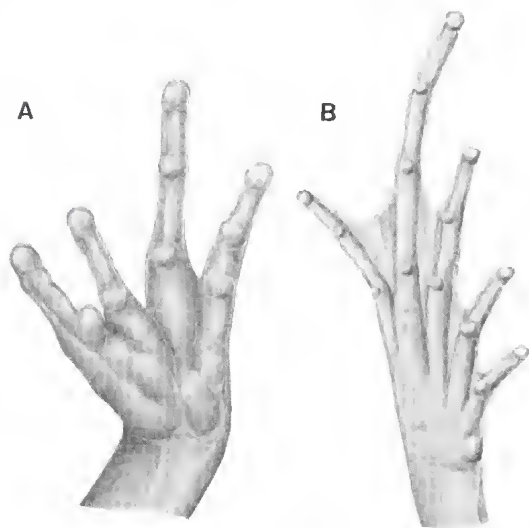


Fig. 14. A. Palmar view of hand and B, plantar view of foot of *Litoria tornieri* (SAM R19572).

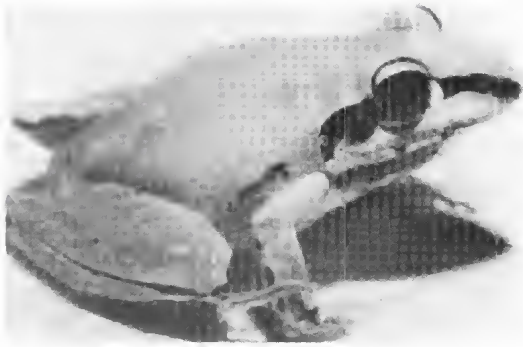


Fig. 15. *Litoria tornieri*, in life (Jabiru, N.T.).

tubercles prominent. Hind limbs moderately long (TL/S-V 0.59). Toes in order of length  $4 > 3 > 5 > 2 > 1$  (Fig. 14). Webbing reaching subarticular tubercle on penultimate phalanx of toe 4. Subarticular tubercles prominent. Small oval inner and tiny rounded outer metatarsal tubercles.

Dorsum smooth, abdomen coarsely granular. Submandibular area smooth and pigmented. Moderately well developed tarsal fold on proximal portion of tarsus. Poorly developed supratympanic fold.

Colour in preservative, brownish grey with conspicuous very dark headstripe; anteriorly to nostril, headstripe extending diffusely to tip of snout; between eye and nostril headstripe sharply delineated and interrupted by pale preocular bar (Fig. 2) behind eye, stripe extending above and through tympanum to insertion of forearm; two dark patches prominent in axillary region. Broad white stripe from preocular bar to posterior extremity of mandible.

Backs of thighs heavily pigmented by continuous dark bands separated by continuous stripe and occasional patches of pale ground colour (Fig. 4).

Continuous dark brown stripe along outside edge of tibia and ventral surface of tarsus. Prominent dark brown patch on wrist and edge of forearm.

Well developed glandular nuptial pad on thumb.

*Material examined:* Holotype, BMNH 1947.2.22.73, Port Essington, N.T., and 50 other specimens. Northern Territory: SAM R18653-73, Jabiru Airstrip; SAM R18687, R16779. Katherine R., 7 km W Katherine Gorge; SAM R9072, 5 km N Mainoru; SAM R14775E,C, 16 km S Hooker; SAM R18679, Cannon Hill; SAM R18682,

Birndu; SAM R18685, E Gulungul Ck; SAM R18683, Arnhem Highway nr Mudginberry Fence; SAM R18684, Coonjimba Billabong; SAM R18680-1, Retention Pond No. 2, Djalkmarra Ck; SAM R19572, Buffalo Billabong, 9 km NW Jabiru; AM R32071-3, R32114-6, Port Essington; SAM R18676-7, 16 km S Woolner; SAM R18678, Berry Ck; UAZ A232, Batchelor, Finnis River; UAZ A523-4, A610-2, Jabiru Airstrip; Western Australia: WAM R57194, Pago Mission Ruins, Mission Cove, Napier-Broome Bay; WAM R50670-1, Drysdale R. N.P., 14°44'S, 126°56'E,

### Variation

Small frog (males 27-34 mm, females 28-36 mm). Head longer than broad (HL/HW  $1.23 \pm 0.12$ , 1.09-1.35). Head length  $1/3 - \frac{1}{2}$  snout to vent length (HL/S-V  $0.37 \pm 0.02$ , 0.31-0.42). Hind limbs short (TL/S-V  $0.57 \pm 0.04$ , 0.49-0.68). Anterior head region relatively broad with variable E-N/IN ( $0.75 \pm 0.10$ , 0.61-1.03).

As indicated by these measurements, *L. tornieri* exhibits limited variation in body form and has the shortest hind limbs of all members of the *L. latopalmata* species group.

In colouration, *L. tornieri* is the least variable member of the species group. Mottling of the dorsal and dorsolateral surfaces has not been observed, but in preservative the colour tends to fade and varies from brownish to grey. This variation is probably a reflection of the breeding condition of the specimens as sexually mature calling males tend to be a distinct reddish-brown colour.

The uninterrupted, narrow, dark stripe on the anterior edge of the tibia is consistently present and is an excellent character distinguishing this species from sympatric members of the *L. latopalmata* species group. However, the dark pigment spots in the axilla are sometimes absent.

### Osteology

Skull relatively fragile with moderately ossified neurocranium. Sphenethmoid moderately ossified extending between but not anteriorly to nasals dorsally and just anteriorly to dentigerous processes of premaxillae ventrally. Nasals lying alongside not overlapping sphenethmoid (Fig. 16A). Prootic and exoccipital fused. Exoccipital not ossified dorso- or ventromedially. Crista parotica well developed, short and stocky. Otic ramus of squamosal not articulating with distal extremities. Frontoparietal fontanelle extensive,

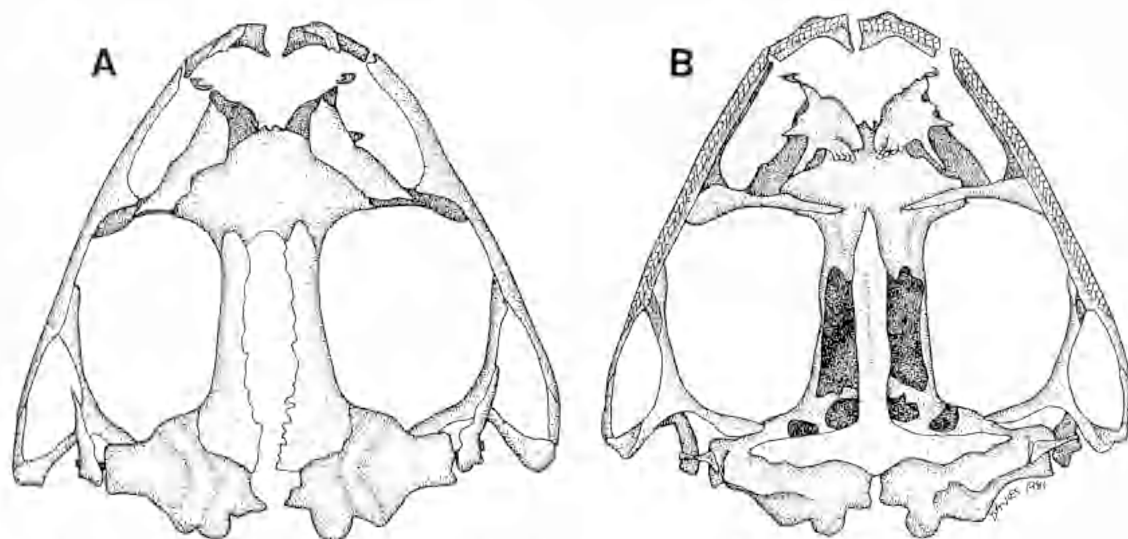


Fig. 16. A, Dorsal, and B, ventral views of skull of *Litoria tornieri* (UAZ A681).

reaching anteriorly to level of palatines; posteriorly undelineated because of lack of medial ossification of exoccipital. Orbital edges of frontoparietals straight.

Maxillary process of nasals moderately sharp, not articulating with well developed preorbital process of pars facialis of maxillary. Palatines expanded distally, slender medially overlying sphenethmoid. Parasphenoid slender; cultriform process long, slender reaching between palatines; alae long, at right angles to cultriform process and overlapped by medial arm of pterygoid.

Pterygoid moderately robust, in moderately long contact with moderately developed pterygoid process of palatal shelf of maxillary. Medial arm long, not in bony contact with prootic region.

Quadratojugal slender, fully articulated. Squamosal slender, otic ramus expanded and slightly longer than acuminate zygomatic ramus. Maxillary and premaxillary dentate. Preorbital process of moderately shallow pars facialis of maxillary well developed. Alary processes of premaxillaries elongate laterally, curved posterolaterally. Palatal processes of premaxillaries well developed, not abutting medially. Prevomers slightly reduced medially. Dentigerous processes short, angled slightly to midline. Bony columella present.

Pectoral girdle arciferal and moderately robust. Omosternum and xiphisternum present. Clavicles slender, equal in length to scapula

and abutting medially. Coracoids moderately separated. Suprascapular about 2/3 ossified.

Eight procoelous nonimbricate presacral vertebrae. Medial dorsal ossification incomplete on presacrals I, II, III and IV. Relative widths of transverse processes III > IV > II > sacrum > V > VI > VIII > VII. Sacral diapophyses moderately expanded, ilia extending anteriorly beyond expansion. Bicondylar sacrococcygeal articulation. Well developed crest extending  $\pm$  length of urostyle.

Phalangeal formula of hand 3,3,4,4; well developed bony prepollex. Phalangeal formula of foot 3,3,4,5,4; well developed bony prehallux. Terminal phalanges knobbed.

#### Variation

Well expanded otic ramus of squamosal lies alongside crista parotica in some specimens. Pterygoid process of palatal shelf of maxillary absent to variously developed.

#### Breeding Biology

*Call:* Males call from cover either under leaves or at the base of grass tussocks within 3 m of water. At Jabiru, N.T., males were heard calling in early November and early March (Tyler *et al.* 1983). Calls are well tuned, with most of the energy below 2000 Hz (Table 1, Fig. 6).

*Early development:* Tyler *et al.* (1983) describe eggs and larvae of this species. Embryos at stage 20 and larvae at stage 33 are illustrated in Fig. 17.

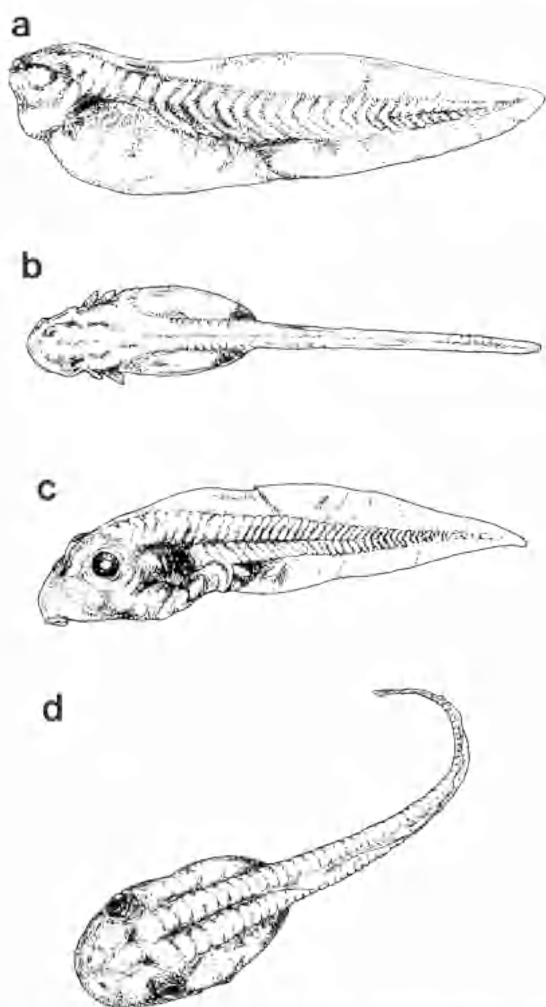


Fig. 17. a, Dorsal and b, lateral views of embryo at stage 20, c, dorsal and d, lateral views of larva at stage 33, of *Litoria tornieri*. Total length of embryo 4.5 mm, body length 2.3 mm, total length of larva 28.5 mm, body length 11.0 mm.

#### Distribution

*Litoria tornieri* has the most restricted distribution of the ground hylid species (Fig. 7). The type locality is Port Essington on the Coburg Peninsula in the Northern Territory and the species is confined to the north of the Northern Territory and Western Australia. The southernmost record is 16 km S of Hooker, N.T. The species is an open forest dweller and is sympatric with *L. inermis* and *L. pallida* at Jabiru, N.T.

#### Comparison with other species

*Litoria tornieri* can be distinguished from all terrestrial congeners, other than the *L. aurea*,

*L. freycineti* and *L. latopalmata* species groups, by the unexpanded terminal discs on the fingers and toes. From members of the *L. aurea* group it can be distinguished by their gross size and habitus and from the *L. freycineti* group by relatively shorter hind limbs. From *L. pallida*, *L. inermis* and most specimens of *L. latopalmata*, *L. tornieri* can be distinguished by the presence of an uninterrupted brown stripe on the outer side of the tibia. From those specimens of *L. latopalmata* possessing such a stripe, *L. tornieri* can be distinguished by its less expanded discs (not extending laterally beyond the fringes of the penultimate phalanx), its smaller size (males 27–34 mm, females 28–36 mm, compared with males 29–39 mm, females 36–42 mm) and its relatively shorter hind limbs (TL/S-V  $0.57 \pm 0.04$  in *L. tornieri*,  $0.64 \pm 0.03$  in *L. latopalmata*). *L. tornieri* has longer short calls than any other member of the group.

#### *Litoria pallida* sp. nov.

FIGS 2, 4, 6, 18–22

*Litoria latopalmata*: Tyler 1968 (*pariim*) p. 719

**Holotype:** SAM R19555, a male collected at Gulungul Creek Crossing, Arnhem Highway, N.T., 12°39' S, 132°52' E, by G. A. Crook on 10.xii.1978.

**Definition:** A small highly variable ground dwelling species (female 31–37 mm, male 27–34 mm) characterised by unwebbed fingers, poorly expanded fingers discs, first finger considerably longer than second; long hind limbs (TL/S-V  $0.62 \pm 0.04$ ); well developed stripe on side of head; smooth or mottled dorsum, sometimes faintly tubercular.

**Description of holotype:** Head longer than broad (HL/HW 1.18); head length more than one third snout to vent length (HL/S-V 0.38). Snout prominent, projecting in profile (Fig. 2) and slightly rounded when viewed from above and in profile. Nostrils more lateral than superior, distance from end of snout  $\frac{1}{2}$  that from eye. Distance between eye and naris equal to internarial span (E-N/IN 1.00). Canthus rostralis moderately well defined and straight, its nature accentuated by dark rostral stripe. Eye relatively small and inconspicuous, diameter slightly greater than eye to naris distance. Tympanum completely visible, diameter about  $\frac{1}{2}$  eye diameter (Fig. 18).



Fig. 18. *Litoria pallida*, in life (Jabiru, N.T.).

Vomerine teeth on short oval elevations between anterior edges of choanae. Tongue broadly oval.

Fingers moderately long and slender lacking lateral fringes (Fig. 19A); in order of length  $3 > 1 > 4 > 2$ . Fingers unwebbed. Terminal discs poorly developed, not extending beyond lateral extremities of penultimate phalanx. Subarticular and palmar tubercles prominent. Many supernumerary tubercles present.

Hind limbs long (TL/S-V 0.62). Toes in order of length  $4 > 3 > 5 > 2 > 1$  (Fig. 19B). Webbing reaches midpoint of penultimate phalanx on toe 5 and to level of subarticular tubercle at base of antepenultimate phalanx of toe 4. Subarticular tubercles prominent. Small oval inner and smaller rounded outer metatarsal tubercles.

Dorsum smooth; abdomen, pectoral region and undersurface of thighs coarsely granular; submandibular area smooth. Well developed proximal tarsal fold; moderately developed supratympanic fold.

Colour in preservative: dorsum grey and hind limbs brown with conspicuous very dark stripe extending from nostril to eye, interrupted

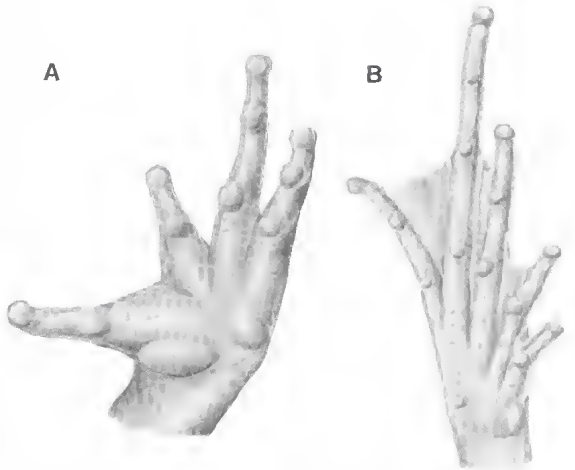


Fig. 19. A, Palmar and B, plantar view of hand and foot of *Litoria pallida* (SAM R19539).

by a white preocular bar. Posteriorly stripe extends through and above tympanum, terminating above insertion of forearm. Disrupted dark spots extend halfway along flank. White stripe extends from lower margin of eye to insertion of forearm.



Thigh markings dark, separated from ground colour by pale yellow patch contiguous with irregular dorsal margin; dark markings commonly disrupted and extensively marked by lighter markings (cf. Fig. 4). Disrupted brown patches extend along edge of tibia; plantar surface of tarsus and foot uniformly brown.

Brown, glandular, bilobed nuptial pad; throat moderately suffused with pigment.

*Dimensions of holotype:* S-V 31.7 mm; TL 19.7 mm; HL 12.0 mm; HW 10.2 mm; E-N 3.1 mm; IN 3.1 mm; E 3.7 mm; T 2.9 mm.

*Etymology:* The specific name is derived from the Latin *pallidus* meaning pale, ashen, in reference to the predominant colour of the dorsum.

### Variation

There are 121 paratypes:

Northern Territory: SAM R19539, 4 km W Baralil Ck, 30.xi.1978, G. A. Crook, M. Davies, M. J. Tyler (illustrated); SAM R19549, 40 km N Elliott, 16.xii.1980, M. Davies, A. A. Martin, M. J. Tyler; SAM R19451-4, Jabiru Airstrip, 7.xii.1979, G. A. Crook; SAM R19455-7, Jabiru Airstrip, 4.xi.1978, G. A. Crook; SAM R19458, R19491-504, 30 m N Retention Pond No. 2, Djalkmarta Ck, Ranger Uranium Lease, 5.xii.1979, G. A. Crook; SAM R19459-62, small pools, 100 m upstream Coonjimba Billabong, 5.xii.1979, G. A. Crook; SAM R19463, R19474-90, Cannon Hill, 1.viii.1976, M. King; SAM R19464, soak from ore body, Jabiru, 29.xi.1978, M. Davies, M. J. Tyler; SAM R19465, 4 km W Baralil Ck, 30.xi.1978, M. Davies, M. J. Tyler; SAM R19466-9, McArthur River bridge on road to McArthur R. Str., 24.ix.1979, G. A. Crook; SAM R19470-1, Gulungul Swamp, 150 m SE Gulungul Ck Crossing, Arnhem Highway, 1.ii.1979, G. A. Crook; SAM R19472-3, 800 m W Gulungul Ck Crossing, Arnhem Highway, 1.ii.1979, G. A. Crook; SAM R19506, Coonjimba Billabong, 23.x.1978, G. A. Crook; SAM R19507, Jabiru Airstrip, 29.xi.1978, M. Davies, M. J. Tyler; SAM R19511-3, Collyer Lagoon, Carpentaria Highway, 26.ix.1977, G. A. Crook, W. Zeidler; SAM R19514-33, Lake Woods, nr Elliot, 5.x.1977, G. A. Crook, W. Zeidler; SAM R19540-48, Bullman Hstd, 8.viii.1966, R. Edwards; SAM R9062-3, 133 km N Manora, 23.viii.1967, R. Edwards, Fleming; SAM R14775, R19508-9, 16 km S Hooker, 5.vi.1975, A. Robinson; AMNH 108333-4, Coonjimba Billabong, 23.x.1978, G. A. Crook; WAM R73573, Ja Ja borrowpit at entrance to Pan-Continental Campsite, 28.xi.1977, M. Davies, M. J. Tyler; KU188433-4, Cannon Hill, 28.xi.1977, M. Davies, M. J. Tyler; AM R97183-5, Ja Ja borrowpit nr Pan Continental Camp, 28.xi.1977, M. Davies, M. J. Tyler; NTM R10098-9, Cannon Hill, 28.xi.1977,

M. Davies, M. J. Tyler; QM J39256-8, Ja Ja borrowpit at entrance to Pan Continental Campsite, 28.xi.1977, M. Davies, M. J. Tyler; SAM R19550-1, Jabiru Airstrip, 10.i.1981, M. Cappel, M. Davies, M. J. Tyler (cleared and stained); SAM R19552, 100 m E Jim Jim turnoff, Arnhem Highway, 9.i.1981, M. Cappel, M. Davies, M. J. Tyler, G. F. Watson (cleared and stained); SAM R19553-4, roadside pool, 800 m W, Gulungul Crossing, Arnhem Highway, 1.ii.1979, G. A. Crook (cleared and stained).

Queensland: SAM R14774, R19510, 19 km N Laura, 23.x.1974, A. R. Robinson; QM J41013-6, J41018, Coen Airport, 6.iii.1979, R. G. Atherton, K. R. McDonald; QM J41019, Lakefield N. P., nr Lakefield Hstd, 25.ii.1981, B. J. Lyon, K. R. McDonald (recorded); QM J41017, Coen Airport, 6.iii.1979, R. G. Atherton, K. R. McDonald (recorded).

Western Australia: SAM R19535, Camballin, 18.ii.1980, M. Davies, A. A. Martin, M. J. Tyler; SAM R19536-8, 175 km E Broome, 17.ii.1980, M. Davies, A. A. Martin, M. J. Tyler; WAM R73574, 30-35 km S Duncan Highway/N Highway Jcn, 5.ii.1978, A. A. Martin, M. J. Tyler; WAM R73577, Hidden Valley, Kununurra, 1.ii.1978, M. Davies, A. A. Martin, M. J. Tyler; WAM R73575, Camballin, 18.ii.1980, M. Davies, A. A. Martin, M. J. Tyler; WAM R73576, 175 km E Broome, 17.ii.1980, M. Davies, A. A. Martin, M. J. Tyler.

Adult males measure 27-34 mm and females 31-37 mm. Hind limb length is variable, but usually moderately long  $0.62 \pm 0.04$ ,  $0.53-0.72$ ; head length is always longer than head width ( $1.29 \pm 0.06$ ,  $1.17-1.42$ ) and the head length is always greater than one third of the snout to vent length ( $HL/S-V$   $0.39 \pm 0.02$ ,  $0.36-0.42$ ). Eye to naris distance to inter-narial span ratio highly variable ( $E-N/IN$   $0.89 \pm 0.10$ ,  $0.68-1.12$ ) but usually less than 1.

Variation occurs in dorsal colouration and texture. In some specimens dorsum grey/brown with brown mottlings (Fig. 18), in others, dorsum and dorsal surface of thighs grey. Disrupted dark markings along edge of tibia not always present, nor are markings on anterior surfaces of thighs. Mottling on back can be conspicuous or patchy. In some specimens dorsum weakly tubercular with tubercles aligned longitudinally along back. White stripe below eye appears cream in some specimens and well-developed variegations can be found around lips.

### Osteology

Skull moderately well ossified; sphenethmoid well ossified extending to anterior ex-

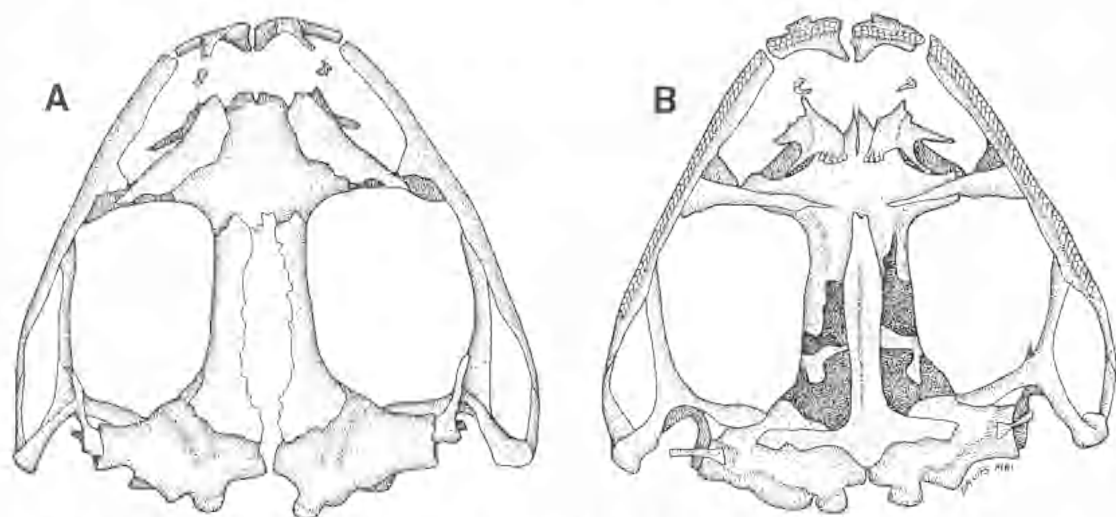


Fig. 20. A, Dorsal and B, ventral view of skull of *Litoria pullida* (SAM R19553).

trémities of nasals dorsally and just anteriorly to dentigerous processes of prevomers ventrally. Nasals overlying sphenethmoid along their medial edges. Prootic and exoccipital fused but medial fusion absent in exoccipital. Crista parotica moderately well developed, short and stocky, barely overlapped laterally by moderately expanded otic ramus of the squamosal. Frontoparietal fontanelle extensive, reaching anterior extremity of orbit (Fig. 20A). Posterior margin undelimited due to lack of medial fusion of exoccipital. Orbital edges of frontoparietals straight.

Nasals moderately large, widely separated medially. Maxillary processes acuminate and articulate with well developed preorbital process of pars facialis of maxillary. Palatines expanded distally, very slender and acuminate medially overlying sphenethmoid.

Parasphenoid robust. Cultriform process moderately broad, irregularly truncate and reaching almost to level of palatines (Fig. 20B). Alae moderately long, at right angles to cultriform process and barely overlapped by medial arm of pterygoid. Pterygoid moderately robust. Anterior arm in moderately long contact with poorly developed pterygoid process of palatal shelf of maxillary. Medial arm slightly expanded distally.

Quadratojugal slender and fully articulated. Squamosal moderately robust. Zygomatic ramus slender and slightly shorter than moderately expanded otic ramus of squamosal. Maxillary and premaxillary dentate. Palatine

processes of premaxillaries well developed, not abutting medially. Alary processes of premaxillaries elongate laterally, curved posterolaterally. Prevomers reduced slightly medially. Dentigerous processes short, horizontally oriented. Bony columella present.

Pectoral girdle aciferal and moderately robust. Omosternum and xiphisternum present. Clavicles slender and abutting medially. Coracoids moderately separated. Scapula slightly shorter than clavicles. Suprascapula about 2/3 ossified.

Eight procoelous, nonimbricate, presacral vertebrae. Medial, dorsal ossification incomplete on vertebrae I, II, III and IV. Relative widths of transverse processes: III > IV > II > sacrum > V > VI > VII > VIII. Sacral diapophyses moderately expanded, ilia extend anteriorly beyond the expansion. Sacrococcygeal articulation bicondylar. Well-developed crest extending for about 1/2 length of urostyle.

Phalangeal formula of hand 3,3,4,4. Well-developed bony prepollex. Phalangeal formula of foot 3,3,4,5,4. Well-developed bony prehallux. Terminal phalanges claw shaped.

#### Variation

Well-developed preorbital process of pars facialis of maxillary not always articulating with maxillary process of nasal. Distal expansion of medial arm of pterygoid not occurring to same extent in all specimens. Degree of ossification of sphenethmoid varies and hence its relationship with nasal and prevomers.

### Breeding Biology

*Call:* Males call in open areas within 1 m of water. At Jabiru, N.T., males were first heard calling in early November, and last heard in early March (Tyler *et al.* 1983).

This species shows the greatest differentiation between long and short calls, with the former having at least 10 times the duration of the latter (Table 1, Fig. 6). There are complex frequency shifts and multiple harmonic bands in both calls, and a considerably more exhaustive analysis is required to fully elucidate the call structure.

*Early development:* Tyler *et al.* (1983) have described development in this species (as

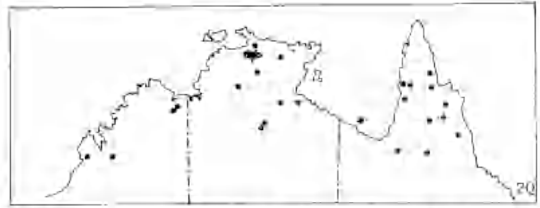


Fig. 22. Distribution of *Litoria pallida* in Australia. Star indicates type locality.

"*Litoria* sp. nr *latopalmata*"). An embryo at stage 20 and a larva at stage 34 are illustrated in Fig. 21.

### Distribution

*Litoria pallida* is confined to the north of Australia from Broome in W.A. to Cape York in Qld, above latitude 20° (Fig. 22). Like the other ground hylid species it is an open forest dweller and is sympatric with *L. inermis* on Cape York and *L. tornieri* and *L. inermis* at Jabiru, N.T.

### Comparison with other species

*Litoria pallida* can be distinguished from all terrestrial congeners except the *L. aurea*, *L. freycineti* and *L. latopalmata* species groups by the unexpanded discs on the fingers and toes. It can be distinguished from members of the *L. aurea* group by its size and habitus and from the *L. freycineti* group by its relatively shorter hind limbs.

From *L. tornieri*, *L. pallida* can be distinguished by the absence of a continuous stripe along the outside edge of the tibia, and by its relatively longer legs (TL/S-V  $0.62 \pm 0.04$  in *L. pallida*,  $0.57 \pm 0.04$  in *L. tornieri*). It can be distinguished from *L. latopalmata*, the species with which it has been confused, by its smaller size (males 27–34 mm, females 31–37 mm compared with 38–37 mm males and 36–42 mm females in *L. latopalmata*) and poorly expanded discs which do not project beyond the lateral edges of the penultimate phalanges of fingers and toes. *Litoria pallida* can be distinguished from *L. inermis* by its well-developed lateral headstripe, strongly marked thighs and relatively smooth dorsum. As mentioned above, the call structure of *L. pallida* is particularly distinctive.

*Other material examined:* QM J27228, 12 mile Creek on Normanton–Karumba Rd. Qld; QM J28916, Norman Creek Rd to Norman; QM J31369, along Glen Esk Rd near Esk. Qld; SAM R9710, Strathgordon Hstd Qld, SAM R9720, Edward River Hstd Qld; SAM R9660, Edward

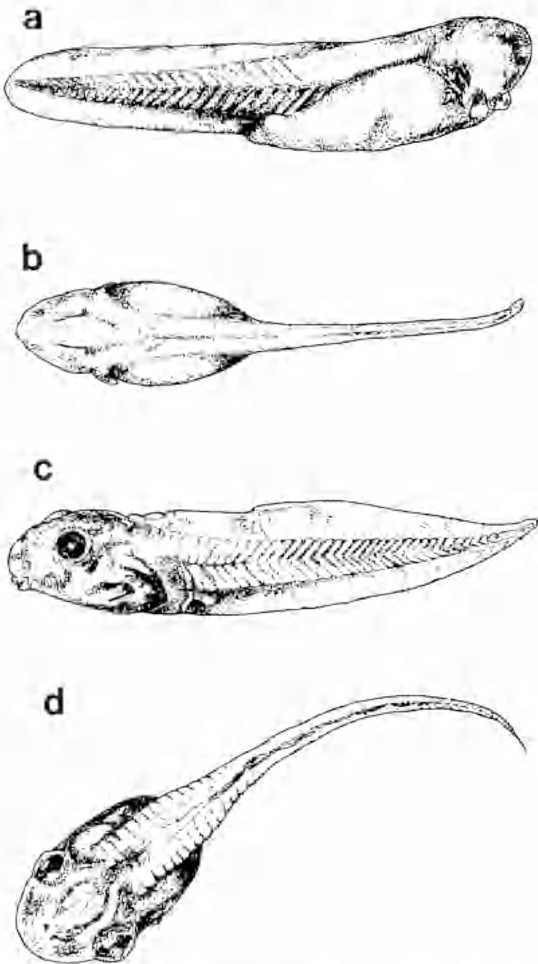


Fig. 21. a, Lateral and b, dorsal view of embryo at stage 20, and c, lateral and d, dorsal view of larva at stage 34, of *Litoria pallida*. Total length of embryo 4.4 mm, body length 2.3 mm, total length of larva 30 mm, body length 10.5 mm.

River, Qld; SAM R4935 Mornington Island; SAM R8174, R19534, Mulliman Hstd, N.T.; WAM R62889-62898, upper reaches McKinley River, N.T.; SAM R19632-47, McArthur River Bridge on road to McArthur River Stn; SAM R19622-31, Lake Woods, nr Elliott, N.T.; SAM R19614-21, Collyer Lagoon (just off Carpentaria Highway), N.T.; SAM R19655-68, Coomalie Creek, 25 km N Adelaide River, N.T.; SAM R9417, Mitchell River Mission, Qld; SAM R9680, R9699, Hann River, N. Qld; SAM R9885, R9876, R9841, Stralhgordon Hstd, Qld; SAM R9714, Edward River Stn, Qld; SAM R9718, Laura River, Qld; SAM R9868, R9852, Hann River/Kennedy Rd, Qld.

### Discussion

Many cryptic species have been described amongst those frogs exhibiting wide geographic ranges across the north of Australia and down the eastern seaboard. Since Moore's (1961) definitive work on the frogs of New South Wales, *Litoria bicolor* (Gray), *Cyclorana australis* (Gray) and *C. brevipes* (Peters) have been shown to consist of such cryptic species pairs resulting in the resurrection or description of *L. fallax* (Peters), *C. novaehollandiae* Steindachner and *C. longipes* Tyler & Martin.

Ground hylids of the *Litoria latopalmata* species group have for a long time been a taxonomic enigma, particularly because most museum material is poorly preserved and consists of subadult specimens. This latter situation is the result of collections being made in the dry season, when many northern areas are accessible. For this reason, we have not included some of the material examined by us in the type series but have indicated its existence in the text.

The members of the *L. latopalmata* species group are extremely homogeneous in their morphology, osteology, calls and developmental history. Intraspecific variation is common in characters that are usually morphologically reliable such as rugosity of the dorsum, delineation of canthal stripes, tibial markings, back pattern, toe webbing (Moore 1961, Fry 1913, Copland 1955, Tyler 1968b) and development of supernumerary sub-articular tubercles. Osteologically the four species are very conservative. Interspecific differences are slight and often ontogenetically controlled, therefore being of little value.

The call structure is unusually complex among Australian frogs. Neither a typical call sequence nor a typical call duration can be

defined, since calls are produced in very long series of heterogeneous notes. Our categorization of call notes as long and short represents only a first step in describing the acoustic repertoire. It is probable that different behavioural roles are served by the different call elements; it may be, for instance, that short calls have a territorial and long calls a courtship function. However the severe limitations of our data preclude further speculation.

From what is known of other hylid signalling systems, it is probable that pulse repetition rate is a key component indicating species identity (Littlejohn, 1971). The sympatric eastern taxa, *L. latopalmata* and *L. inermis* show clear differences in pulse repetition rate of both long and short calls, though the temperature variation in our samples makes definitive comparisons impossible. *L. inermis* also shows consistent differences in pulse repetition rate from *L. tornieri* and *L. pallida*, but the pulse repetition rate of the latter two is more similar. However they are markedly different in both number of pulses per note and note duration.

Larvae are very similar and typical of Australian *Litoria* (Martin & Watson 1971). *Litoria inermis* larvae can be distinguished from those of *L. pallida* and *L. tornieri* by the dorsal rather than lateral position of the eyes. *Litoria pallida* and *L. tornieri* larvae are indistinguishable until metamorphosis.

Failure to recognize the taxonomic complexity of this group has led to many anomalies in the literature. Andersson (1913) for instance, reported *Chiroleptes inermis* and *Hyla affinis* from the Kimberley Division of Western Australia. The former specimen is readily referable to *L. inermis* as the description and illustration provided are clearly recognisable. The latter specimen cannot be identified from the written description and may represent either *L. tornieri* or *L. pallida*, both of which occur in the area.

Tyler's (1968b) study of frogs of the *L. lesueurii* complex in northwestern Australia included representatives of all three northern species, as *L. latopalmata*. However, Tyler delineated specimens from southern and central Queensland and northern N.S.W. from all other specimens by the degree of dilation of discs, the more extensive webbing and development of supernumerary tubercles on the palmar and plantar surface of the hands and feet exhibited by these specimens. These

are the only non-fugitive characters that we have found reliable in our own analysis. Straughan (1969) referred to Andersson's specimens in his redefinition of *L. inermis* (as *Hyla inermis*) and commented on the relatively shorter tibia length compared with Queensland specimens. He considered this difference to be trivial in view of the wide geographic range of the species. Our studies have shown this difference to be exceedingly constant within the northwestern Australian specimens.

Of the 120 specimens measured from the Northern Territory and northern Western Australia only 13 had a TL/S-V  $\geq$  0.59. The mean was  $0.57 \pm 0.03$  with a range of 0.51–0.67. The Queensland specimens showed consistently longer hind limbs (TL/S-V  $0.63 \pm 0.04$  (0.56–0.68 range)) (see Fig. 8). Adams *et al.*<sup>1</sup> could not separate the populations electrophoretically and we cannot separate the calls of the two populations. Hence all specimens are referred to *L. inermis*.

Cogger & Lindner (1974) remarked that the types of *Litoria latopalmata* and *L. inermis* were indistinguishable. These specimens are in poor condition and distinguishing characteristics have become blurred, although the syntype of *L. inermis* housed at the American Museum of Natural History and collected at Bowen is clearly identifiable as that species.

Since both species are sympatric at their type localities and since modern usage of the names *L. latopalmata* and *L. inermis* in reference to species found in N.S.W., southern Queensland and South Australia causes no confusion (Moore 1961, Cogger 1979, Barker & Grigg 1978, Tyler 1977, 1978), it would invite nomenclatorial chaos to question the validity of the current application of the names *L. latopalmata* and *L. inermis*.

The *L. latopalmata* species group definition of Tyler & Davies (1978) should be modified in the following ways:

Dorsum brown, grey or reddish, usually bearing extensive irregular markings of little if any recognisable pattern.

Nasals well developed and separated widely medially. Frontoparietal fontanelle extensive; crista parotica well developed, short and stocky; otic ramus of squamosal slightly expanded, usually lying alongside crista parotica;

palatines expanded laterally, slender distally; prevomers reduced slightly medially, denticulate processes short; preorbital processes of moderately shallow pars facialis of maxillary well developed; palatine processes of premaxillaries well developed, not abutting medially; alary processes of premaxillaries extended laterally and inclined posterolaterally; quadratojugal fully articulated; otic ramus of squamosal generally slightly longer than zygomatic ramus; parasphenoid large, alae long and at right angles to cultriform process; maxillary and premaxillary dentate; bony columella present.

Pectoral girdle arciferal and moderately robust; slender clavicles abutting medially; phalangeal formula of hand 3,3,4,4; well developed bony prepollex; phalangeal formula of foot 3,3,4,5,4; well developed bony prehallux; eight procoelous nonimbricate presacral vertebrae; dorsal ossification on anterior three vertebrae always incomplete; transverse processes of presacral vertebrae long; sacral diapophyses moderately expanded; ilia extending anteriorly to expansion; well developed urostyle crest extending 2/3 to 3/4 length of urostyle; sacrococcygeal articulation bicondylar.

*Composition:* Four species are included in the group: *Litoria latopalmata* Günther, *L. inermis* (Peters), *L. tornieri* (Nieden) and *L. pallida* sp. nov.

#### Key to species in *Litoria latopalmata* species group

1. Dorsum tubercular, lateral headstripe poorly defined, thigh markings finely reticulated *L. inermis*  
Dorsum usually smooth, lateral headstripe well defined, particularly before the eye, thigh markings strongly reticulated 2
2. Finger discs not extending laterally beyond edge of penultimate phalanx 3  
Finger discs extending beyond edge of penultimate phalanx *L. latopalmata*
3. Stripe along edge of tarsus interrupted *L. pallida*  
Stripe along edge of tarsus uninterrupted *L. tornieri*

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<sup>1</sup> Adams, M., Baverstock, P. R., Tyler, M. J. & King, M. Genetic differentiation among Australian frogs of the family Hylidae. Unpubl. ms.

British Museum (Natural History) for type of *L. latopalmata* and *L. tornieri*, Queensland Museum for Queensland ground hylid representatives, Rijksmuseum van Natuurlijke Historie, Leiden for a syntype of *L. inermis*, and the South Australian Museum for access to its extensive collection of ground hylid material. We are grateful to Graeme Crook, Max King, Greg Miles, Michael Mahony and Keith McDonald for the provision of fresh material and to Graeme Crook and Keith McDonald for calls and field notes of some Northern Territory and Queensland species respectively. Chris Miller is thanked for hours of painstaking tadpole rearing, Linda Trueb is responsible for the superb illustrations in Figures 2,3,9,14 and 19. Tadpole illustrations

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